

THE SIMPLE LEAVED LUPINES AND THEIR RELATIVES IN ARGENTINA¹

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ABSTRACT

Arguments are presented to support the thesis that leaves of lupines with a single blade are simple rather than unifoliate. Three species in Argentina have all or some of their leaves simple. *Lupinus guaraniticus* and *L. sellowianus* have only simple leaves, whereas *L. paraguariensis* has simple leaves at the base of the plant and the first leaf of each lateral branch but the others are palmately compound. Three related species with palmately compound leaves are treated in this paper: *L. albescens*, *L. aureonitens*, and *L. multiflorus*.

The species of *Lupinus* are restricted to the New World, with the exception of a limited number in the Mediterranean region, and a few in Africa, reviewed by Gladstone (1974), and Plitmann (1981). The major speciation centers are in the montane western area of North America, Mexico, and in the Andean region of South America. The simple-leaved lupines occur mainly in the central and southeastern region of Brazil. Four species were treated by Small (1933) as the *Simplicifolii* in Florida. Dunn (1971) contended that the four taxa of the complex originated in Brazil and reached Florida by long range dispersal.

The species treated in this paper are the only known biennial or perennial lupines in northeastern Argentina that are related to lupines of Brazil, Paraguay, and Uruguay. Their floral or vegetative characteristics are not remotely similar to those of Andean lupines. The other three native species that grow in the area are annuals.

DISCUSSION OF LEAF CHARACTERISTICS IN *LUPINUS*

Different terminology has been used to describe the simple-blade leaf of lupines. Whether they should be considered simple-leaved or unifoliate has been an unresolved question.

Bentham (1859), in his treatment of *Lupinus* in "Flora Brasiliensis," used the characteristics "leaves simple or unifoliate" in the same statement of the key, without any subsequent separation or explanation about the difference. How-

ever, in the following genus, *Crotalaria*, he clearly separated simple-leaved species from unifoliate species. He defined "Simplicifoliae" as those having leaves with one blade sessile or with a narrow petiole without articulation. In contrast, the "Foliolatae" are defined as having leaves with one to three leaflets, with the petiole articulate at the apex.

Smith (1945) recognized 21 simple-leaved lupines for Brazil and referred to them as unifoliate. Burkart (1952, 1967) also used the term unifoliate in his description of *Lupinus*.

Hutchinson (1964), in the key to the tribe Lupineae, separated *Lupinus* by the characters "leaves simple, digitately several to many-foliate or 1-foliate." Later in the description of the genus he stated "very rarely digitately 3-foliate or 1-foliate."

Polhill (1976) considered the leaves of *Lupinus* "5-11(-17)-foliate or less often (in Central and South America) 1-3-foliate." However, Bisby (1981) described the subtribe Lupinae (with only one genus, *Lupinus*) with "leaves 5-17-foliate, palmate, rarely simple."

This literature review shows that there is not an unanimous opinion in the use of appropriate terminology to describe the simple-blade leaves of *Lupinus*. To resolve the problem, we studied the morphology of the leaves using the same criteria of the articulation or abscission of the petiole introduced by Bentham (1859) in *Crotalaria*. The position of the abscission layer can readily be determined from old leaves of preceding years.

The perennial species of *Lupinus* with digi-

¹ The work was a portion of the problems encountered by A. M. Planchuelo (1978) in her doctoral dissertation under the direction of D. B. Dunn at the University of Missouri-Columbia.

² Division of Biological Sciences, University of Missouri-Columbia, 202 Tucker Hall, Columbia, Missouri 65211. The authors wish to express their appreciation to the curators of the herbaria that were cited in the distributions. Without the study of the type material and the illustrations, the work would not have been possible.

tately compound leaves commonly have the abscission layer at each petiolule or base of each leaflet, at the top of the petiole. In many species the petioles remain attached to the plant at least one year before finally weathering away. In other species the petiole is lost shortly after the fall of the leaflets, by a later abscission at the base of the petiole. In contrast, in the simple-leaved species of *Lupinus*, abscission occurs only at the base of the petiole or where the petiole becomes free from the fusion of the stipules. After abscission there is often a flange-like remnant remaining at the node where the leaves from the previous year were attached. However, there is no visible indication of an abscission zone at the top of the petioles of the 18 species of simple-leaved lupines that we have been able to study from Brazil, Paraguay, and Argentina. There are several species that have completely lost the entire petiole, in which case there is an abscission below the sessile blade.

We concluded from this study that the term unifoliolate is not appropriate for the genus *Lupinus*, hence, we considered the simple-blade leaves as truly simple.

An interesting condition in *L. paraguariensis* shows a transitional stage between simple and compound leaves. The juvenile basal leaves from the caudex, and the first leaf produced on the lateral branches, are simple. The other leaves of the main stems and branches are digitately compound with three to five leaflets. The compound leaves do not show any sign of abscission zone at the base of the leaflet or at the top of the petiole, and the petioles do not remain attached to the plant as in other species. *Lupinus paraguariensis* is the only known species with the combination of simple and compound leaves in mature plants.

We were able to obtain some viable seeds of *L. albescens*, and all of the seedlings in the colony we planted produced one simple elliptical leaf blade on the first leaf above the cotyledons. The second leaf had three leaflets, the third had five leaflets, and the number of leaflets increased as the vigor of the seedling increased, until the typical number of the mature plants developed, as cited in the section on taxonomy. We are confident that the same situation will occur in *L. aureonitens* and *L. multiflorus*, because they are morphologically closely related to *L. paraguariensis*. None of the North American lupines that we have grown experimentally have germinated with the first leaf simple.

TAXONOMY

Only the perennial or biennial species of north-eastern Argentina, adjacent Brazil, Paraguay, and Uruguay are treated in this paper (Fig. 1). There are three native annual species (*L. bracteolaris* Desr., *L. linearis* Desr., *L. gibertianus* C. P. Smith) and three annuals sometimes cultivated (*L. albus* L., *L. angustifolius* L., *L. luteus* L.) in this area that are not included. The leaves in this group are simple or compound with well-developed pinnate lateral venation. The plants are herbaceous and generally die back to a perennial caudex, with the exception of *L. guaraniticus* (Hassl.) C. P. Smith, which may become sprawling and suffruticose. The stipules are well developed in all of the species except *L. guaraniticus*, in which the free tips are absent. The tapered base, as well as the absence of a gibbous base of the upper-lip of the calyx, is very similar in all of the species of this group, and sets them apart from the Andean lupines, in which the gibbous base is often well developed. The tooth-like tip of the wings and the conformation of the banner also suggest that the species in the group are closely related.

KEY TO THE SPECIES

- 1a. Leaves all or some simple.
 - 2a. Leaves all simple.
 - 3a. Stipules with free tips absent; stems ligneous or herbaceous, appressed sericeous; petioles 8–13 mm long; flowers 13–16 mm long 1. *L. guaraniticus*
 - 3b. Stipules with free tips present; stems herbaceous, shaggy-lanate; petioles 20–60 mm long; flowers 10–12 mm long 2. *L. sellowianus*
 - 2b. Leaves simple at the base of the plant and the first leaf of each lateral branch, the others palmately compound 3. *L. paraguariensis*
- 1b. Leaves all compound.
 - 4a. Wing tips rounded, without a tooth-like tip; keel angle over 90° 5. *L. multiflorus*
 - 4b. Wing tips with an upturned tooth-like tip; keel angle 90° or less.
 - 5a. Leaves primarily basal; stems with branches primarily basal; lower leaves generally with three leaflets; leaflets complanate 4. *L. aureonitens*
 - 5b. Leaves primarily cauline; stems erect, branching above; all leaves of mature plants with 5–12 leaflets, conduplicate 6. *L. albescens*

1. *Lupinus guaraniticus* (Hassl.) C. P. Smith, Sp. Lup. 325. 1943. (Fig. 2). *L. attenuatus* Gardn.

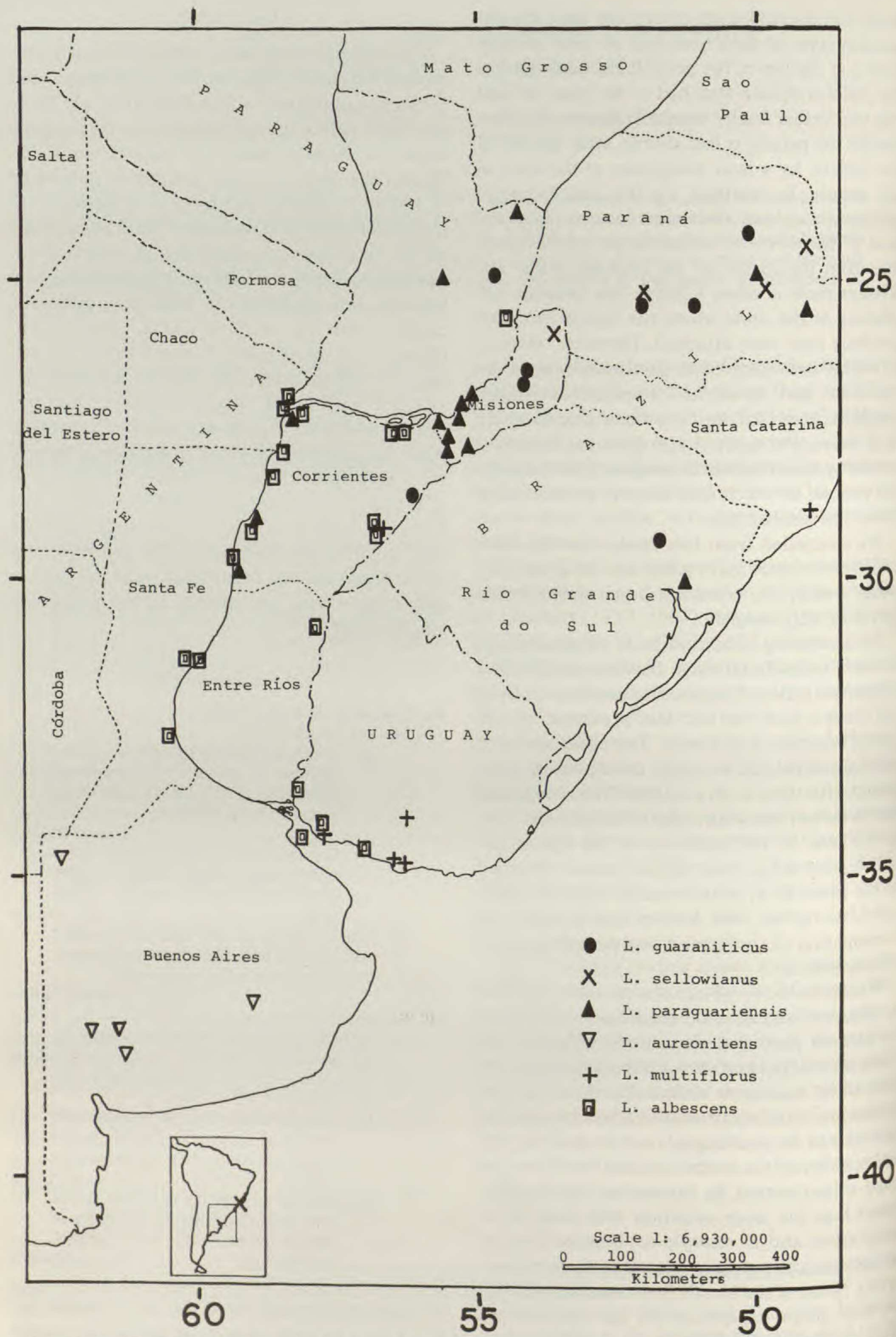
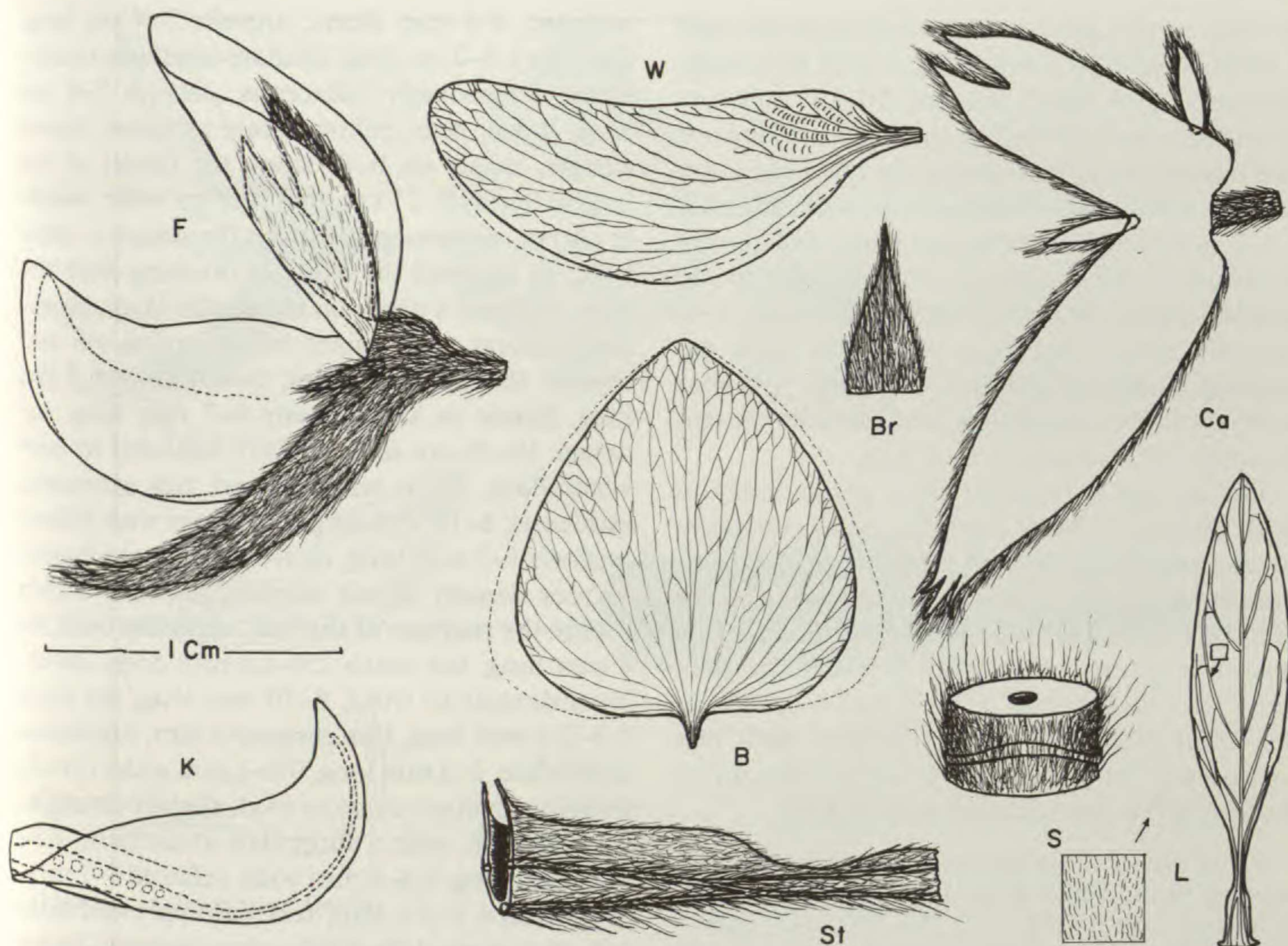


FIGURE 1. Distribution of the simple leaved lupines of Argentina and their relatives as listed in the legend.



Lupinus guaraniticus (Hassler) C.P. Smith

FIGURE 2. Illustration of typical structures of *Lupinus guaraniticus*. The floral and vegetative parts, with the exception of the leaf, are drawn to the scale shown from the mean values of a set of multiple specimen dissections. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened so that the inside surface shows; F = lateral view of the left side of the flower; K = keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn; L = typical leaf (not to scale), the lateral veins drawn from the lower surface view; inset illustrates the thinly strigose hairs of upper surface; S = stem structure showing the flange left after abscission of the leaf; St = stipular portion fused to the petiole with no free portion present; W = wing petal.

var. *guaraniticus* Hassler in Fedde, Repert. Spec. Nov. Regni Veg. 16: 158. 1919. TYPE: Paraguay. In fields, Alto Paraná, Fiebrig 5681 (holotype, G; isotype, SI; photo, UMO).

Plants perennial, 3–7 dm tall, several stems from a branched caudex; stems herbaceous, or becoming ligneous, suffruticose, hollow, 3–6 mm diam., sericeous, hairs of several sizes, tawny in age, the longest hairs 2–3 mm long, internodes 2–4 cm long; stipules with the free tip absent, connate portion sheathing half of the diameter of the stem; petioles 8–13 mm long; leaves simple, entire, lance-elliptic, complanate at maturity, minutely strigose to thinly sericeous above, finely to densely sericeous below, the largest blades 7–9.5 cm long, 1.7–3 cm wide with 4–6 lateral veins on each side arcing forward, tips

acute to obtuse, the base as a narrow wing along the entire petiole, abscission of the leaf near the base of the petiole; peduncles 3.5–6.5 cm long at anthesis, sericeous; racemes 7–11 cm long, flowers scattered; bracts caducous, ovate, sericeous dorsally, 4–6 mm long, 2–2.8 mm wide at the base, tips attenuate; pedicels 2.5–3 mm long at anthesis, 5–6 mm long in fruit, sericeous; calyces sericeous outside, glabrous within, the base slightly or not gibbous above, lower-lip lanceolate, 12–17 mm long, 3–5 mm wide, the tip trifid, central tooth ca. 2 mm long, 1 mm wide, the lateral teeth much shorter and curved outward, upper-lip 8–12 mm long, 3–4 mm wide below, bifid, the notch 2–3.5 mm deep, the lobes 1.5 mm wide, lips connate 1.5–2.5 mm, bracteoles lanceolate, 2–3.5 mm long, 0.7–1 mm wide, attached 0.3–0.6 mm below the lips of the lateral

sinuses; *corolla* glabrous; *banner* oval-ovate with a short claw, 12–15 mm long, 10–13 mm wide, appressed 2–4 mm, reflexed 10–13 mm, reflexed/appressed ratio 3–5, the blade arching out and upward with the sides hardly reflexed; *wings* arcuate, 13–16 mm long, 5–6 mm wide, the claw 1.5–2 mm long, the lobe above the claw poorly developed; *keel* arcuate, 3.5–5 mm wide in the middle, tip acute, curved backward; *ovules* 6–8; *legumes* 5.5–6.5 cm long, 9–10 mm wide, ascending lanate; *seeds* 6–6.5 mm long, 4–5 mm wide, dark brown mottling and speckles on tan, funicular pit elongate, 2 mm long.

The species is reported from grassy areas in open places or slopes from Paraguay, southern Brazil, and Misiones and Corrientes in Argentina. It is viewed as the most primitive species of those treated in this paper, due to the ligneous sprawling stems, which often persist more than one year: other species die back to a woody caudex or function as biennials. The lack of the free tips of the stipules places it out of the direct lineage to the other species treated here.

Representative specimens. ARGENTINA. CORRIENTES: Santo Tomé, Ruta 40 y Arroyo Chimiray, *Schinini & Canevali* 10323 (CTES, MO, UC), *Quarin* 3402 (CTES). MISIONES: San Pedro, En la picada a La Celulosa, *Perrone s.n.* (BA #54259, SI); San Pedro, *Niederlein* 1129 (SI).

BRASIL. PARANA: Arapati, Fda. do Tigre, *Hatschbach* 7206 (US); Castro, Carambei, *Hatschbach* 35482 (BH, CTES); Guarapuara, Aeroporto, *Hatschbach* 30851 (UC); Laranjeiras do Sul, *Hatschbach* 4238, 4239 (US); *Hatschbach* 35213 (BH, CTES, MO, UC); Tibagi, Fda. Mt. Alegre, Invernada Miranda, *Hatschbach* 2822 (US). RIO GRANDE DO SUL: Canabara, S Fr. de Paula, *Rambo* 36207 (MO); Caxias do Sul, no Strede Caxias—V. Oliveira, *Valls* 1431 (CTES); St. Loureiro Gomez, *Bornmuller* 325 (GH); S Angelo, S João Velho, *Pedersen* 11949 (CTES, SI). SANTA CATARINA: Agua Doce, Campos de Palmas, *Smith & Klein* 13612 (US); Curitiba, Campo 11 km SE of Marombas, *Smith & Klein* 12202 (US); Campo Alegre, *Reitz & Klein* 5267, 6165 (US).

PARAGUAY. Itaquigry, alto Paraná, *Fiebrig* 5881 (SI); Regione fluminis, alto Paraná, *Fiebrig* 5681 (G, SI).

2. *Lupinus sellowianus* Harms in Fedde, Repert Spec. Nov. Regni Veg. 17: 5. 1921. TYPE: Brazil. Location unknown, *Sello* 4866 (holotype, B, not seen) (Fig. 3).

Plants perennial, herbaceous, seasonal stems arising from a subsurface root-stalk; *stems* 2.5–4.5 dm tall, hollow, slightly fistulose, loosely shaggy-lanate, lower internodes very short, upper 2–3 cm long, ridged from the veins of the

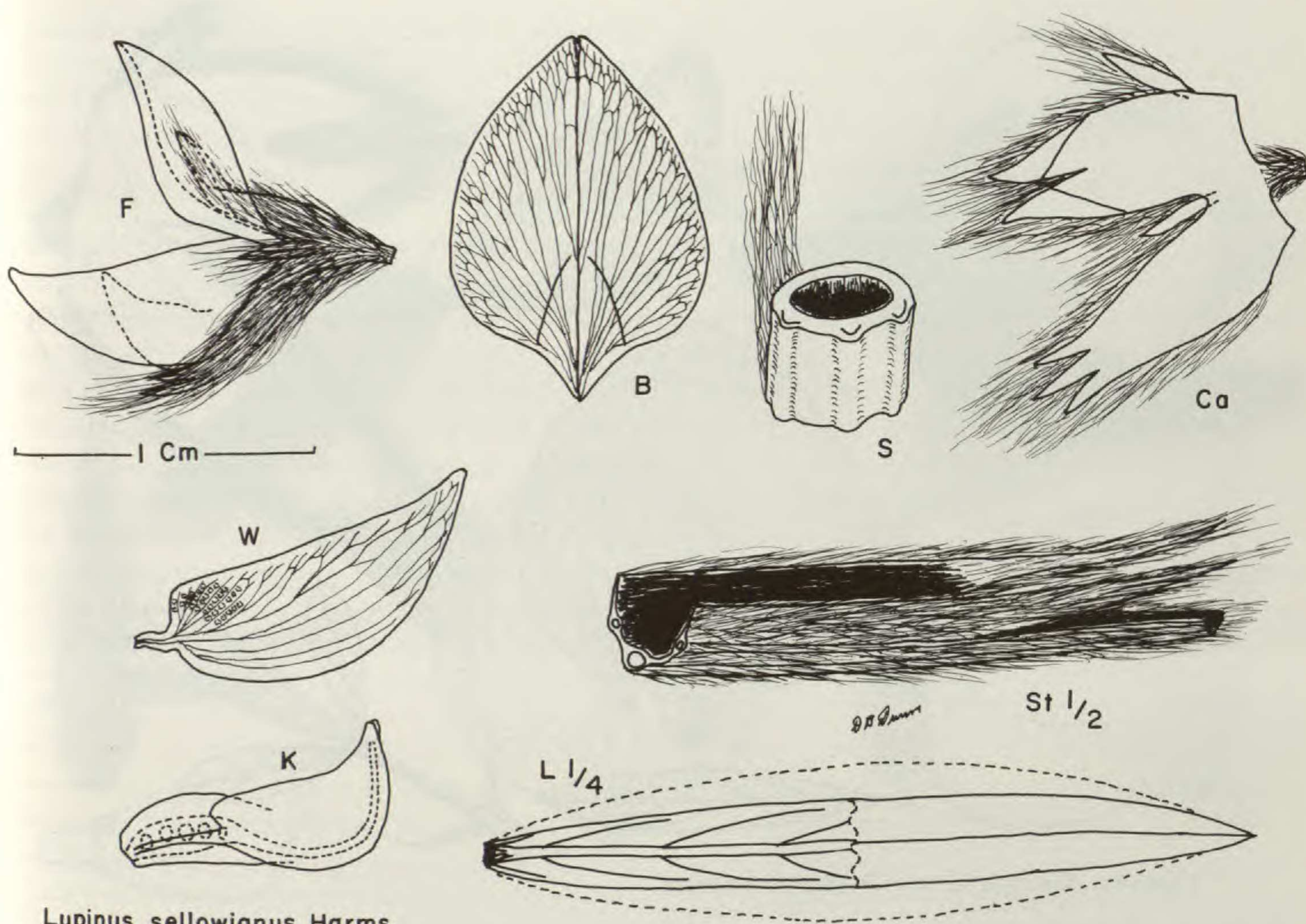
petioles, 3–6 mm diam.; *stipules* 2–4 cm long, free tips 1.5–2 cm long, caudate-attenuate to subulate, occasionally foliaceous; *petioles* 2–6 cm long, longer ones below, lanate as stems; *leaves* simple, lanate on both sides, the blades of the largest leaves 8–11 cm long, 1–2 cm wide, smaller above, not abscissing from the petioles, withering in age and the petioles breaking near the base, without a clear-cut abscission layer, prominent lateral veins raised below, arcing out and toward the tip, 5–8 pairs; *peduncles* 4–6.5 cm long, lanate as stems, hairs 4–7 mm long; *racemes* 10–20 cm long, flowers scattered to subverticillate; *bracts* lance-shaped, tips attenuate, caducous, 8–10 mm long, 2–2.8 mm wide below; *pedicels* 1–2 mm long, densely appressed lanate; *calyces* densely lanate outside, glabrous within except the margins of the lips, upper-lip bifid, 6–8 mm long, the notch 2.8–3.5 mm deep, lower-lip tridentate to trifid, 8–10 mm long, the teeth 1.5–2.5 mm long, lips connate 2 mm, bracteoles lanceolate, 2–3 mm long, 0.6–1 mm wide; *corolla* glabrous; *banner* ovate to oval, slightly emarginate at the tip, with a short claw at the base, 9.8–11.6 mm long, 6.4–8 mm wide, reflexed 6–7 mm, appressed 4.3–5.5 mm, reflexed/appressed ratio 1.3, the angle 120–135°; *wings* narrow, lower margin arcuate, tip pointed, weakly fused distally below the tip, 10.5–11.5 mm long, 3.3–4.7 mm wide, claw 1.5–1.8 mm long, tooth above the claw 1.4–2 mm wide; *keel* 2.5–3.4 mm wide in the middle, the angle 85–90°; *ovules* 4; *legumes* immature, 25 mm long, 6 mm wide, shaggy-lanate.

The floral parts are remarkably similar to those of *L. multiflorus* as well as the leaf venation and indument of vegetative parts. This species is reported for the first time for Argentina.

Smith (1945: 492) cited three specimens of *L. sellowianus* from the Berlin herbarium. One is the type specimen *Sello* 4966, from Brazilia; the second is *Dusen* 13173, from Parana; the third is *Dusen* 7261, from Espirito Santo, which was photographed by mistake as the type specimen, and the picture is filed in the New York herbarium. These three specimens were apparently destroyed by fire in Berlin in WWII.

Representative specimens. ARGENTINA. MISIONES: Bernardo de Irigoyen, 7 km en camino a San Pedro, *Krapovickas et al.* 23381 (CTES).

BRASIL. ESPIRITO SANTO: Villa Velha, *Dusen* 7261 (photo NY); Laranjeiras do Sul, *Hatschbach* 35218 (UC); Ponta Grossa, *Hatschbach* 17390 (UC). SAO PAULO: S Pedra Campos, *Lofgren* 319 (RB).



Lupinus sellowianus Harms

FIGURE 3. Illustration of typical structures of *Lupinus sellowianus*. The floral parts and the section of the stem are drawn to the scale shown from the mean values from dissections of specimens cited. B = banner petal flattened, dorsal view; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; K = keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn; L = average largest leaf (drawn to $\frac{1}{4}$ of the scale shown), lateral veins of the lower surface drawn on the lower half; S = stem structure, first year growth, vascular traces from petiole above; St = stipules, detached at the node (drawn to $\frac{1}{2}$ of the scale shown); W = wing petal.

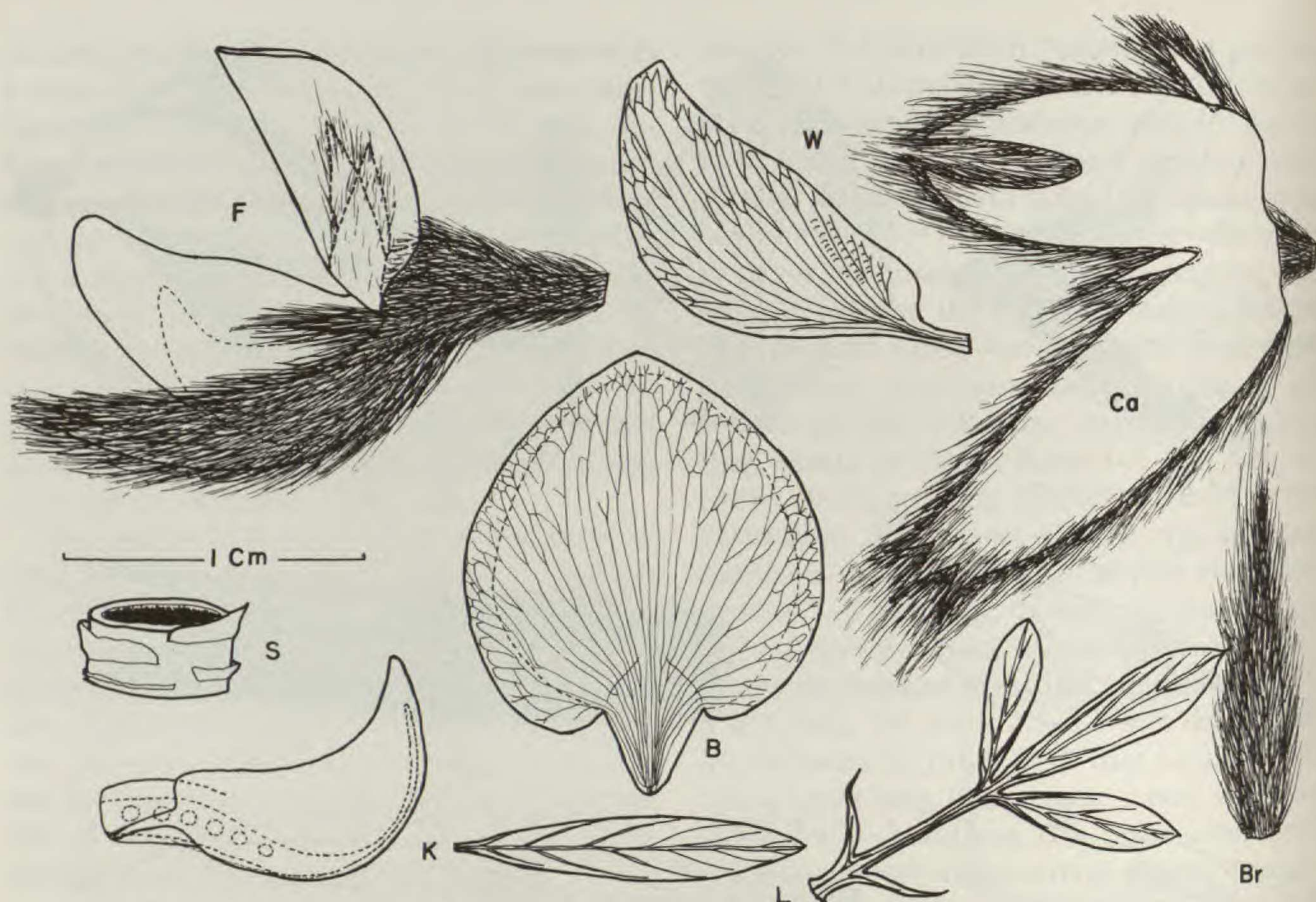
3. *Lupinus paraguariensis* Chodet & Hassler, Bull. Herb. Boissier, Ser. 2, 4: 836. 1904. TYPE: Paraguay. Regione fluminis, Capibary, Hassler 4430 (holotype, G; isotypes, GH, LIL, MO, NY, UC; photos, F, GH, UMO) (Fig. 4).

L. paraguariensis var. *missionum* Hassler in Fedde, Repert. Spec. Nov. Regni Veg. 16: 159. 1919. TYPE: Argentina. Misiones: fields near San Ignacio, Hassler 445 (holotype, G).

L. missionum (Hassler) C. P. Smith, Sp. Lup. 325. 1943.

Plants perennial, possibly biennial, 4–8 dm tall; stems fistulose, 6–8 mm diam., appressed woolly pubescence to 5 mm long, with an undercoat of shorter hairs, internodes 2–8 cm long; stipules 2–5.5 cm long, the free tips slender, 1.5–4.5 cm long, lanate; longer petioles 6–12 cm long, lanate; leaves simple at the base of the plant and the first

leaf on each branch, the others 3–5 palmately compound, leaflets broadly elliptical to elliptical-oblongate, complanate at maturity, appressed lanate on both surfaces, the largest 10–13 cm long, 1.8–4.5 cm wide, midribs and pinnate lateral veins conspicuous, tips obtuse, mucronate; abscises near the base of the petiole or at the point where the stipules become free; peduncles 4–7 cm long, lanate; racemes 12–30 cm long or little longer after fully developed, flowers scattered or subverticillate; bracts deciduous, narrow, lanceolate, 8–15 mm long, 1–2.5 mm wide below, lanate dorsally, tips long-attenuate; pedicels 2–4 mm long at anthesis, 6–7 mm long in fruit, lanate; calyces appressed lanate outside, glabrous within, except the tips and margins of the lips, lower-lip oblong, arcuate, 13–18 mm long, 4–6 mm wide, tips trifid, the teeth similar, 1–3 mm long, 0.4–0.8 mm wide, upper-lip 9–13



Lupinus paraguariensis Chodet & Hassler

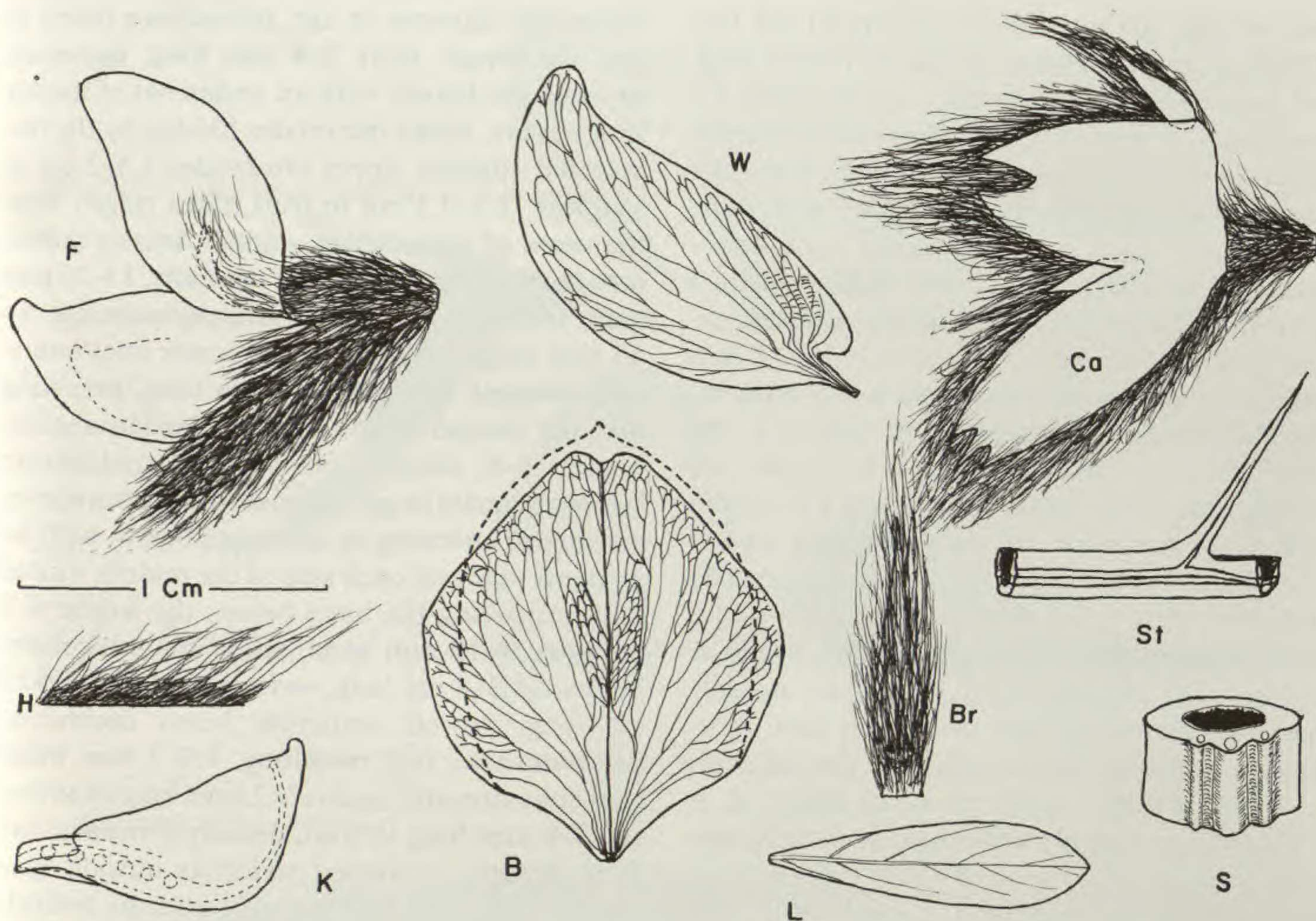
FIGURE 4. Illustration of the typical structures of *Lupinus paraguariensis*. The floral and vegetative parts, except the leaves, are drawn to the scale shown, from the mean values of a set of multiple dissections, from the geographic range of the species from specimens cited. B = banner petal flattened, dorsal view; Br = bract, dorsal view; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; K = keel petals enclosing the staminal tube and pistil, with the mean number of ovules drawn; L = leaflet and trifoliolate leaf (not drawn to scale), note leaflets often connected by lamina at base, petiole often with a wing; S = stems fistulose, with flanges left where leaves abscised, in some areas they weather away; W = wing petal.

mm long, bifid, the notch 3.5–6 mm deep, each lobe 2 mm wide, lips connate 2.5–3.5 mm, bracteoles lanceolate, tips attenuate, 2.5–4 mm long, 0.4–0.7 mm wide, attached at the lips of the lateral sinuses, both lips elongating after fertilization; corolla glabrous; banner oval, 14–15 mm long, 10–13 mm wide, appressed 4.5–5.5 mm, reflexed 8–9 mm, reflexed/appressed ratio 1.8, the angle 113° , the top part arcing forward; wings 13–15 mm long, 5–6 mm wide, the claws 2–3 mm long, the lobe above the claws poorly developed, the blade arcing upward distally as a broad blunt tip; keel 3.5–4.5 mm wide in the middle, the tip strongly hooked backward; ovules 6–7; immature legumes to 4 cm long, 8 mm wide, densely shaggy-lanate; seeds not seen.

The species occurs in southern Brazil, Paraguay, and Argentina. It is found in open areas or along river banks, and flowers in early spring. The similarity of floral traits to those of *L. guaraniticus* and *L. velutinus* of Brazil clearly suggests

that they are all related. The variety *missionum*, named by Hassler, represents only younger plants or those in less favorable ecological situations. Field studies are needed to verify this.

Representative specimens. ARGENTINA. CORRIENTES: Candelaria, entre San Ignacio y Santa Ana, Cabrera et al. 29362 (SI, UMO); Capital, Riachuelo, arenal alto de Yatay-pony, Schinini & Ahumada 12368 (CTES); Empedrado, Río Empedrado, ruta 12, Krapovickas et al. 19961 (CTES); Esquina, Estancia Santa Bárbara, Carnevalli 3368 (CTES); Ituzaingó, Isla Apipé Grande, Schinini & Vanni 15784 (CTES); Lavalley, ruta 12, 7 km N de Enpalme con ruta 120, Tressens et al. 651 (CTES); Santo Tomé, Estancia San Juan Bautista, Krapovickas et al. 26015 (CTES). MISIONES: Apóstoles, Pueblo Apóstoles, Ibarrola 1091 (GH); cruces rutas 201–203, 30 km NE of Apóstoles, Krapovickas et al. 15470 (CTES, UC); Loreto, Loreto, Burkart 4586 (GH), Gruner 1028 (BAF); San Ignacio, Alrededores, Pfeiffer 111 (CTES); Posadas alrededores, Spegazzini 10811 (BAF); San Ignacio, Hassler 445 (G, type of var. *missionum*), Muniez 114 (BAF); 5 km de San Ignacio, camino al Teyu-Cuare, Quarín 3477 (CTES); San Ja-



Lupinus aureonitens Gillies

FIGURE 5. Illustration of the typical structures of *Lupinus aureonitens*. The floral and vegetative parts are drawn to the scale shown from the mean values of the limited number of specimens cited. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened so that the inside surface shows; F = flower, left lateral view; H = stem hairs, multiple sizes; K = keel petals, enclosing the staminal tube and pistil, with the average number of ovules drawn; L = average largest leaflet (not drawn to scale), lateral veins of lower surface shown; S = stem structure, first year, varies to fistulose, vascular traces show on the internodes from the petiole above; St = stipule, detached at the node, not abscissing; W = wing petal.

vier, 11 km NE de San Javier, Krapovickas & Cristobal 28870 (CTES).

BRAZIL. PARANA: Entrada Curitiba, Ponta Grossa, Proxima Rio Papagaio, Pereira 6112 (RB); Ponta Grossa, Parque Villa Velha, Hatschbach 8752 (RB). RIO GRANDE DO SUL: Sao Leopoldo, Leite 553 (NY).

PARAGUAY. Condillere de Peribebui, Balansa 3109 (BAF); Regione Fluminis, Yhu, Hassler 9498 (F, NY, UC); Sierra de Maracayú, regione fluminis, Capibary, Hassler 4430 (F, GH, LIL, MO, NY, UC); Valenzuela, Rojas 12841 (BAF).

4. *Lupinus aureonitens* Gilles in Hooker, Bot. Misc. 3: 201. 1833. TYPE: Argentina. Buenos Aires: Pampas near Cabeza del Tigre (K, not seen) (Fig. 5).

L. purolantus C. P. Smith, Sp. Lup. 343. 1944. TYPE: Argentina. Buenos Aires: Sierra Tampé, Sierra de la Ventana, Lorentz 3 (holotype, US; isotypes, CORD, F).

Plants biennial, or possibly sometimes annual,

or a short lived perennial, 15–20 cm tall in fruit, branches mostly basal; stems ligneous and hollow, 6–10 mm diam., densely soft subappressed to spreading lanate throughout all vegetative parts, tawny in age, longer hairs 5–7 mm long, with a dense undercoat of kinky hairs 2.5–4 mm long, upper internodes 1.8–3 cm long at fruiting, the lower not elongated; stipules 2.5–4 cm long, free tips 1.5–2 cm long, the lower ones imbricated for ca. 7 cm; petioles 5–8 cm long, persistent long after the leaflets drop; leaflets 3–6, oblanceolate, mostly complanate, 4–6 lateral veins on each side of the midrib, hidden in the dense lanate hairs, largest leaflets 4–6 cm long, 8–18 mm wide, tips obtuse, mucronate; peduncles 2–4 cm long; racemes 12–20 cm long in fruit, flowers scattered; bracts deciduous, densely lanate dorsally, lanceolate, tips caudate, 6 mm long, 2 mm wide below; pedicels 2–5 mm long at anthesis, 6–8 mm long in fruit; calyces densely la-

nate outside, glabrous within except at the tips of the lips, lower-lip lance-oblong, 9–10 mm long, 3–4 mm wide, tridentate, the central tooth 1.5 mm long, 0.5 mm wide, the lateral teeth shorter, upper-lip 7–8 mm long, 4–5 mm wide, bifid, the notch 1.5–2 mm deep, the lobes 1.5–2 mm wide, lips connate 2.5–3 mm, bracteoles lance-attenuate, 3–4 mm long, 0.7–1 mm wide, attached 0.5 mm below the lips of the lateral sinuses; *corolla* glabrous; *banner* oval-obovate, 10–13 mm long, 8–12 mm wide, appressed 6–6.5 mm, reflexed 7 mm, reflexed/appressed ratio 1.1, the angle 120–135°, the tip bilobed, or entire, the teeth 0.5 mm long, 1 mm wide; *wings* 12–14 mm long, 5.5–6 mm wide, the tip ending as a lobe or tooth-like, the claw 2–2.5 mm long, the lobe above the claw 1.5–2 mm wide; *keel* 3.5–4 mm wide in the middle, the angle 85–88°; *ovules* 6; *legumes* 4–5 cm long, 8–9 mm wide, densely shaggy-lanate; *seeds* light tan, much dark mottling, 5 mm long, 4 mm wide, the funicular pit 1.3–1.5 mm diam., angle mark not observed.

The species appears more similar morphologically to *L. paraguariensis* in many traits but has the vegetative habit similar to *L. multiflorus*. The leaflet venation and indument are more like *L. paraguariensis*. The distribution is primarily south of Buenos Aires. The leaves with three leaflets are generally basal or the first leaves on the lateral branches. The reduction in the number of the leaflets in the basal leaves suggests relationship with *L. paraguariensis*.

Representative specimens. ARGENTINA. BUENOS AIRES: Tandil, Certos, *Grondona* 8016 (BAA); Cerros Heusser y Clavez, *Hicken s.n.* (SI #5883); General Villegas, *Parodi* 13385 (BAA, SI); *Cabera* 5694 (SI); Sierra Tampé, Sierra de la Ventana, *Lorentz* 3 (CORD, F, US), *Hauman s.n.* (BAA #2285, SI), *Hicken s.n.* (SE #5882); Saavedra, Sierra de Bravard, Abra Hinojo, *Gomez et al. s.n.* (BAA #11346).

5. *Lupinus multiflorus* Desr. in Lam., *Encyclopedia* 3: 624. 1789. TYPE: Uruguay. Montevideo, *Commerson* (holotype, P; flowers and leaflets loaned) (Fig. 6).

L. multiflorus Desr. β . *grandiflorus* Benth. in Mart., *Fl. Brasil.* 1: 16. 1859. TYPE: Unknown.

L. multiflorus Desr. γ . *paucifolius* Benth. in Mart., *Fl. Brasil.* 1: 16. 1859 (holotype, K; photo, UMO).

Plants perennial, short lived, branching basal, with the leaves primarily basal, rosette at ground level when the primary raceme reaches anthesis; *stems* elongate some by fruiting, usually only the upper 2–4 internodes, 5–7 mm diam., hollow,

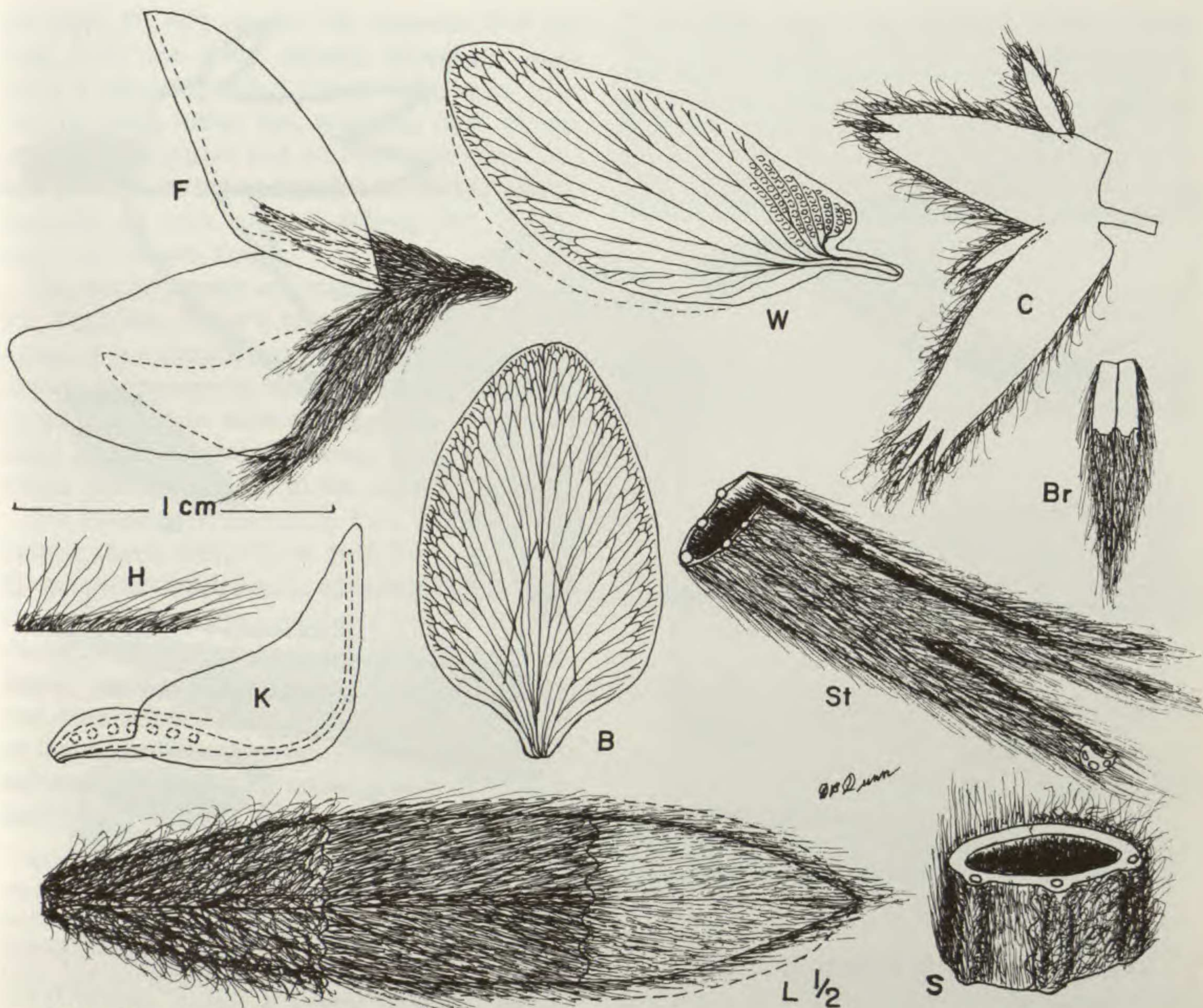
somewhat ligneous in age, pubescence tawny in age, the longer hairs 2–4 mm long, appressed sericeous to lanate, with an undercoat of shorter kinky hairs, lower internodes hidden by the imbricated stipules, upper internodes 1.5–2 cm at anthesis, 2.5–3.5 cm in fruit, three ridged from the veins of the petioles; *stipules* densely pubescent dorsally, sparsely pilose ventrally, 15–26 mm long, free tips narrowly triangular-subulate, 8–15 mm long, 2 mm wide, the lower ones imbricate; longest *petioles* 8–11 cm long, persisting into the second season after the leaflets abscise; *leaflets* 5–8, elliptic-oblongate, conduplicate but complanate in age, strigose to sericeous above, appressed sericeous to sublanate below, with 4–6 lateral veins on each side of the midrib, visible after removing the hairs below, the largest 4–7 cm long, 6–15 mm wide, tips acute, mucronate; *peduncles* 3–8 cm long, sericeous; *racemes* 8–25 cm long, flowers scattered; *bracts* deciduous, lance-caudate, 6–7 mm long, 1.5–2 mm wide, sericeous dorsally; *pedicels* 2 mm long at anthesis, 5–8 mm long in fruit, densely sericeous; *calyces* densely appressed sericeous outside, glabrous within, the base tapering into the pedicel, not gibbous, lower-lip lance-shaped, 8–11 mm long, 2–3 mm wide, tridentate, the teeth 1.5–2 mm long, central largest, upper-lip 6–8 mm long, 3 mm wide, bifid, the notch 1–1.5 mm deep, lobes 1–1.5 mm wide, lips connate 2 mm, bracteoles lanceolate, 2.5–3 mm long, 0.5–0.8 mm wide, attached close to the margins of the lateral sinuses; *corolla* glabrous; *banner* oblong-ovate, 12–16 mm long, 7.5–10 mm wide, appressed 6–7.5 mm, reflexed 5.5–7 mm, reflexed/appressed ratio 0.88–0.92, the angle 120–130°; *wings* 12–16 mm long, 5–7 mm wide, the claw 2–2.5 mm long, lobe above the claw ca. 2 mm wide; *keel* 2.5–3.5 mm wide in the middle, the angle 95–105°; *ovules* 6–8; *legumes* 4–5.5 cm long, 7–8 mm wide, subappressed sericeous to lanate; *seeds* 5–6 mm long, 4–5 mm wide, tan with brown mottling, funicular pit 1.5 mm diam.

The species occurs in Uruguay and Corrientes, Argentina, growing in sandy or gravelly soils. Only one specimen has been seen from Brazil. The sublanate hairs are sometimes present in this species, which is mostly sericeous.

Representative specimens. ARGENTINA. CORRIENTES: La Cruz, *Burkart* 8189 (SE), *Parodi* 12548 (BAA, GH).

BRAZIL. SANTA CATARINA: Laguna, *Hatschbach* 27205 (NY).

URUGUAY. Colonia, Coll. unknown (BAA #1047);



Lupinus multiflorus Desr.

FIGURE 6. Illustration of the typical structures of *Lupinus multiflorus*. The floral and vegetative parts are drawn to the scale shown from the mean values of a set of several dissections, from the geographic range of the specimens cited. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; K = keel petals, enclosing the staminal tube and pistil, with the mean number of ovules drawn; L = average largest leaflet (drawn at $\frac{1}{2}$ the scale shown), lower portion—lower surface sublanate, middle portion—lower surface sericeous, lateral veins prominent, distal third—upper surface; S = stem structure, first year growth, vascular traces from petiole forming ridges on the internode below; St = stipules, detached at the nodes; W = wing petal.

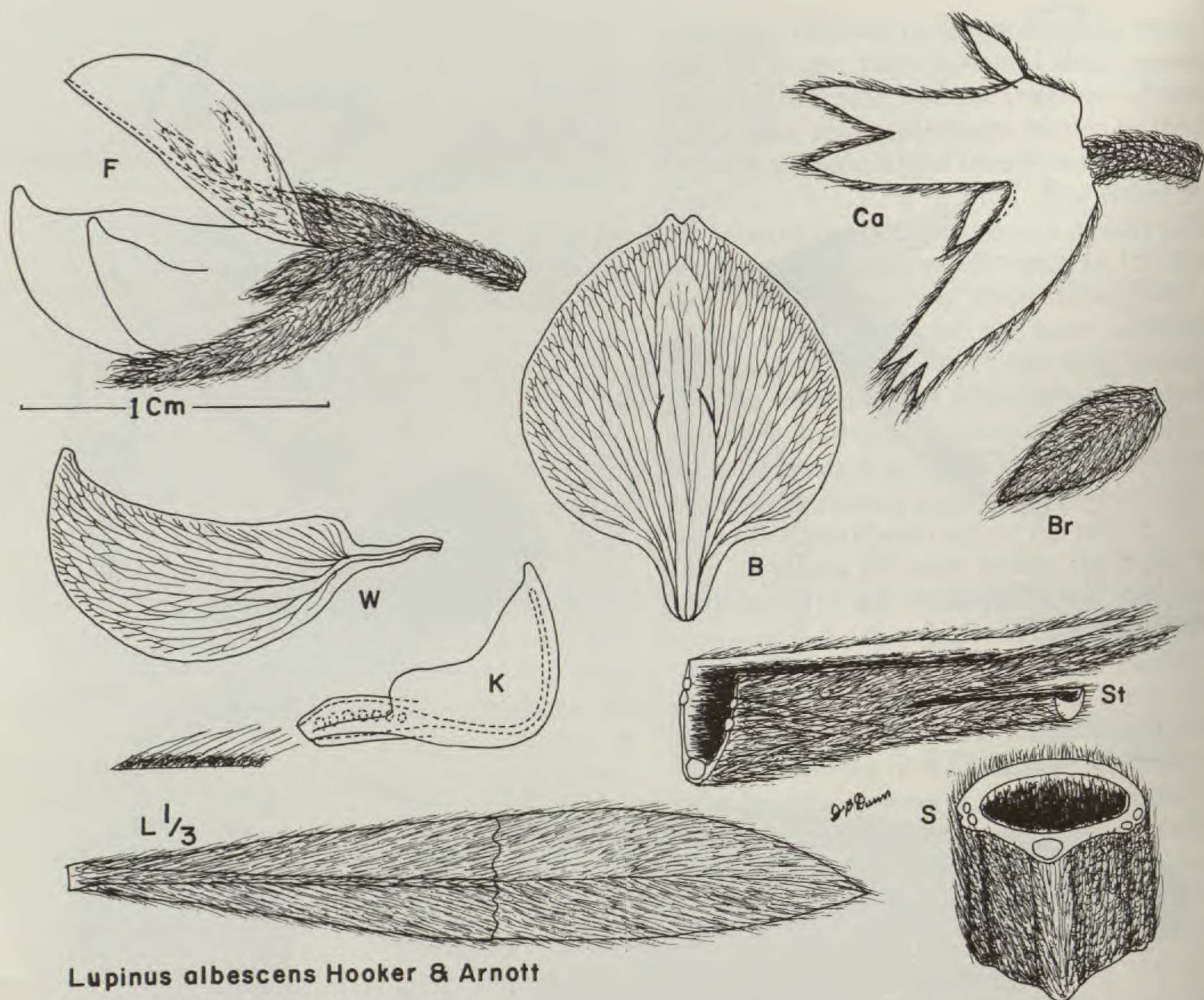
Florida, Cerro Colorado, Ea. San Pedro, Gallinal et al. s.n. (SE# PE 3509); La Valleja, Nico Pérez, Herter 99791 (MO); Montevideo, Commerson s.n. (P); Montevideo, Barattini s.n. (MO #1224502), Berro 1902 (BAF); Independencia, Osten 5632 (SE), Isabelle s.n. (F #153885, NY).

6. *Lupinus albescens* Hooker & Arnott, Bot. Misc. 3: 201. April 1833. TYPE: Uruguay. Unknown, Baird s.n. (holotype, K; H-82/77-7, only the two plants on the right side of the herbarium sheet) (Fig. 7).

L. incanus Graham, Edin. Phil. Jour. 16: 178-179. Dec. 1833.

L. parodianus C. P. Smith, Sp. Lup. 208. 1940. TYPE: Argentina. Buenos Aires: Isla Martin Garcia, Parodi 2530 (holotype, GH; isotype, BAA).

Plants perennial, herbaceous 3-6 dm tall, erect, ramose above; stems hollow, liginous to fistulose, angular, 5-10 mm diam., the hairs yellowish brown, appressed sericeous to sublanate, felt-like mat, longer hairs 2-3 mm long, with a dense undercoat of shorter hairs, upper internodes 2-7 cm long; stipules 10-30 mm long, shortest above, both surfaces densely pubescent, subulate-caudate free tips 7-15 mm long, 1.5 mm wide below; leaves primarily cauline; petioles 7-



***Lupinus albus* Hooker & Arnott**

FIGURE 7. Illustration of the typical structures of *Lupinus albus*. The floral and vegetative parts are drawn to the scale shown, from the mean values of select specimens dissected from within the geographic distribution of the species. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; H = hairs of several sizes; K = keel petals, enclosing staminal tube and pistil, with the mean number of ovules shown; L = average largest leaflet (drawn to $\frac{1}{3}$ scale shown), lower half—lower surface, upper half—upper surface; S = stem structure, first year growth, vascular traces form ridges on the internodes below the petioles; St = stipule, detached at the node; W = wing petal.

16 cm long, pubescent, persisting into the second season after the leaflets abscise; *leaflets* 5–12, oblanceolate, conduplicate or complanate in age, densely sericeous to sublanate on both surfaces, the lateral veins 4–6 pairs, visible below after removing the hairs, the abscission occurs at the base of each leaflet and the petioles persist into the second season; *peduncles* 4–8 cm long; *racemes* 9–40 cm long, flowers verticillate to scattered; *bracts* caducous, ovate-caudate, 6–10 mm long, 2–2.4 mm wide, densely sericeous to lanate dorsally; *pedicels* 4–6 mm long at anthesis, 8–10 mm long in fruit; *calyces* densely sericeous to lanate outside, glabrous within, the base not gib-

bous above, lower-lip lanceolate, 7–10 mm long, 2.5–4.5 mm wide, tip tridentate, the central tooth 2 mm long, 0.6 mm wide, lateral teeth shorter, upper-lip 6–9 mm long, bifid, the notch 1.5–3.5 mm deep, lips connate 1.5–2.5 mm, bracteoles lanceolate, 2–3 mm long, 0.8–1 mm wide, attached from near the lip to ca. 1 mm below the lips of the lateral sinuses; *corolla* glabrous; *banner* obovate, 9–14 mm long, 8–11 mm wide, tip bidentate, the teeth 0.5 mm long, 0.8 mm wide, the angle 130–150°; *wings* 9.5–14.5 mm long, 4.5–6.5 mm wide, the tip with a small tooth-like lobe, the claw 2–3 mm long, lobe above the claw 1.5–2 mm wide; *keel* 3–4 mm wide in the middle,

the angle 80–88°; *ovules* 7–8; *legumes* 6–8 cm long, 8–10 mm wide, densely sericeous; *seeds* 5.8–6.5 mm long, 4.5–5.7 mm wide, sides convex but seeds rather flat, generally dark brown to blackish, stippled and mottled with areas, occasionally more tan and buff than darker colors, funicular pit with large projecting rim, the pit oval 1.2–1.6 mm long.

The species occurs in Uruguay and northeastern Argentina, where it grows in sandy soils and dunes. It is common near Paraná River and on islands. It appears to be the most common perennial species in eastern Argentina. The erect habit clearly separates it from *L. aureonitens*, which also has a tooth at the tip of the wings.

The Hooker Herbarium at Kew has three herbarium sheets (H82/77–6; H82/77–7; H82/77–8) with plants labeled as *L. albescens* Hook. Only the H82/77–7 can be considered the holotype of the species because it specified “Banda Oriental, Baird,” as Hooker and Arnott cited in the original description. The two plants and the leaves on that herbarium sheet are *L. albescens*, but the inflorescence in the left upper corner belongs to another species.

Representative specimens. ARGENTINA. BUENOS AIRES: Isla Martín García, *Cabrera* 2874 (SI), *Parodi* 2526 (CTES), 2530 (BAA, GH). CHACO: San Fernando, Antequera, *Krapovickas & Cristobal* 20066 (CTES, GH); Isla Soto, *Burkart* 30853 (CTES, SE), *Schinini* 16157 (CTES); Acceso al puente Manuel Belgrano, *Schinini* 16024 (CTES). CORRIENTES: Capital, Alrededores de la Ciudad de Corrientes, *Alboff* s.n. (NY); Puente Psoa, *Fernandez* 205 (CTES); Río Riachuelo, *Crovetto* 11116 (CTES); Bella Vista, 10 km S of Bella Vista, *Schinini & Ahumada* 15918 (CTES, MO); Empedrado, “Las Tres Marias,” Río Paraná, *Pedersen* 3049 (GH, MO); Río Empedrado, ruta 12, *Krapovickas et al.* 19959 (CTES); Esquina, Isla frente a Esquina, *Krapovickas et al.* 26899 (BAA, CTES, MO); Ituzaingó, Ituzaingó, *Arbo et al.* 2129 (CTES), *Daciuk* 4 (CTES), *Holmberg* 219 (SI), *Krapovickas et al.* 24471, 24472 (CTES), *Meyer* 6038 (GH, U), *Spegazzini* 10057 (SI); Villa Olivari, *Schinini & Vanni* 15663 (CTES); Paso de los Libres, Paso de los Libres, *Burkart et al.* 29917 (CTES, SI); Laguna Mansa, *Schinini* 7604 (CTES, MO),

7730 (CTES), *Faggi et al.* s.n. (BAA #13983, CTES); Goya, Goya, *Boelcke* 1510 (SI). ENTRE RIOS: Federación, Santa Ana, *Burkart* 28652 (SI), 29337 (CTES); 8 km N, *Burkart* 22588 (SI). SANTA FE: Capital, San José del Rincón, *Burkart* 9056 (SI), *Ragonese* 2441b, 3617 (SI); Altoverde, *Donnet* 2088 (SI); Isla Timbó, en el cruce de balsa de Santa Fe a Paraná, *Burkart et al.* 23699 (SI, UC); Isla Pacará, frente a la capital, *Boelcke & Correa* 9103 (BAA, CTES); Rosario, Rosario, *Burkart* 8774 (F).

PARAGUAY. Puerto Bartoní, alto Paraná, *Jimenez* 7884 (SI).

URUGUAY. Colonia, Riachuelo, *Cabrera* 3938 (F); San José, Arazoti, *LeGrand* 1697 (SI); Soriano, Arenal Grande, *Cabrera* 2571 (NY); unknown, *Baird* s.n. (K, #82/77–7, specimen on right only).

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